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ABSTRACT

The authors surveyed experts in the field of neuro-behavioral research to determine the directions of progress being made in increasing understanding of neural processing and storage of information. Based on this investigation, their report presents examples of research being pursued in this area. The authors see neuro-behavioral research leading to important benefits in preventing or ameliorating the conditions of persons who suffer from impaired learning and memory and also in facilitating or improving the learning of normal individuals. Among the possible research applications discussed are: (1) combating effects of dietary deficiencies on learning and memory; (2) alleviating and preventing mental retardation; (3) preventing or retarding senile decline; and (4) improving the education of normal children in regular schools. The report concludes with suggestions to foster development of research on neural mechanisms of learning and memory and its application. (Author/DOW)

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TRENDS IN RESEARCH ON NEURAL MECHANISMS IN PROCESSING AND STORAGE OF INFORMATION

(A REPORT PREPARED FOR THE NATIONAL INSTITUTE OF EDUCATION)

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I. Methods used in Preparation of this Report

As well as discussing this topic frequently between themselves and with colleagues at Berkeley, the authors undertook three surveys of experts. First was a follow-up survey sent in October 1976 to all participants in the 1974 Asilomar meeting. The following question was asked: "In which directions and by what steps do you expect to see the most important progress made in increasing understanding of neural processing and storage of information?" Twenty-five responses eventually came in, and several of these were detailed and thoughtful statements. In December 1976, we sent a different inquiry to 26 investigators whose names appeared in the 1976 program of the Society for Neuroscience in a section devoted to the topic of Memory and Learning. This inquiry listed the following nine lines of research, derived from the earlier survey and from our own consideration of the field; it asked respondents to select one or more of these lines or to include others of their own choosing and to describe how the approach(es) selected are anticipated to lead to greater understanding of how mammalian brains process, store, and retrieve information:

1. Detailed behavioral descriptions of learning and information processing in different species, using techniques such as signal detection and reaction time analyses.
2. Formal system approaches--block diagrams, artificial intelligence.
3. General chemical, electrophysiological, or anatomical processes that occur in many or all parts of the nervous system during information processing, learning, or consolidation of memory. Examples would be studying synthesis, or widespread electrical patterns that may encode information.
4. Regional localization of neural processes involved in learning and memory. Study of localized electrical or chemical stimulation to modulate information processing or learning.
5. Fine-grained analysis of changes in synapses and neural circuits caused by training.
6. Use of simpler systems--precise chemical stimulation or microelectrode recording in simple organisms, parts of organisms, or tissue preparation.
7. Use of current genetic methods (mapped genes, mutants, mosaics, etc.) to identify enzymes, transmitters, brain tracts and regions involved in learning and memory.
8. Biochemistry of cell-cell interactions on a molecular basis.
9. Study of interaction of genetic determinants and environmental influences in single neurons and in patterns of neural connections.

Only six responses were received, most of these coming from prominent researchers. It did not seem necessary to send out further surveys at this stage.

Many of the replies, especially to the first survey, mentioned only one

or two approaches, and several respondents stated that the approach that they were pursuing in their own research was clearly most likely to yield important advances. On the other hand, several respondents stated that there are many promising directions to be followed and that each should be pursued energetically. A few called for more efforts to integrate findings among levels of analysis, across disciplines, and over different fields of behavior such as perception and motivation as well as learning and memory.

As a third step, in May 1977 we sent a draft of this report to most of the participants of the Asilomar conference and to several other active investigators in this field. This gave an opportunity to those who had replied previously to see what use was being made of the material that they had submitted. It also gave all of those surveyed in the final round an opportunity to make corrections and to offer further suggestions. Sixteen replies reached us in time to be useful in preparing the final report. Thus, while we assume responsibility for authorship of this report, we can at least state that we have consulted a wide range of experts and that the views stated here are more representative than our own personal thoughts about this field.

II. Multiple Research Approaches to Investigation of Neural Mechanisms of Learning and Memory.

A. Introduction

1. Theoretical formulations

There are many different ways in which investigators are trying to formulate the basic neural events that must be involved in learning and storage of memory. Typically, popular formulations at any time in history have often resembled the technology available at that period. Thus, the classical Greeks used as a model for storage of memory their method of making records--marking grooves in the wax coating on a slate (the tabula rasa), Descartes conceived of a hydraulic model based on the hydraulic atomata popular in the 17th century, investigators early in the 20th century used switchboard models based on the telephone system, and some current investigators employ computer models. But as the study of neural processes in learning and memory has become more detailed and sophisticated, different investigators have tended to concentrate on different levels of analysis. By analogy, we can think of the different levels of investigation that are being used to improve our system of transportation by automobile. Among these are studies of the motive force (whether by combustion of fossil fuels or by use of electrical storage batteries); research to improve the mechanical systems; research into appropriate materials, chosen for safety, endurance, weight, and economy; structural design of the vehicle for safety, comfort, and appearance; and traffic engineering for most effective use of automobiles in the overall transportation system. Of course research at each of these levels has implications for the other levels, and an overall view will embrace each of the part views, but each researcher spends most of his or her time in detailed problems at a particular level. Although a person who works on the chemistry of fuel combustion may think of this as the basic question in

automotive transportation, there are certainly many problems of the automobile that cannot be "reduced" to this level of analysis.

Similarly, there are investigators working on problems of neural mechanisms of learning and memory at many levels of analysis, ranging from cell-cell interactions, to activities of circuits or ensembles of neurons, to strategies that learners employ in the coding and retrieval of information. It should be apparent that no one of these is the only or the most important way to consider neural activity in learning and memory. Herbert A. Simon put it in the following way:

> Most of us ... see the natural world as an immensely complex hierarchical system, understandable only by being represented alternatively at many levels of detail, and understood by constructing bodies of theory at each of these levels, in combination with reduction theories that show how the unanalyzed elementary structures at each level can themselves be explained in terms of the constructs available at the next level below. In this world there is need for chemistry as well as physics, biology as well as chemistry, and information-processing psychology as well as physiological psychology. Nor should the necessity for this plurality of levels of theory construction carry any implications for vitalism or mentalism, or bring any aid or comfort to antireductionists. (p. 80, Neural Mechanisms of Learning and Memory, 1976.)

In considering the many research approaches currently being employed to investigate neural mechanisms of learning and memory, the dimension of level of analysis is sometimes confounded with that of the simplicity versus complexity of the particular system being studied. Let us distinguish between these two dimensions, first noting briefly some examples of research going

from small scale and simplicity of the system being studied, at the one pole, to relative completeness and complexity of the system of study, at the other pole. Toward the pole of reduction and simplicity is the study of synaptic formation and function in tissue cultures involving only two cell types, one presynaptic and the other postsynaptic. (This is one of the examples of research to be considered in Section II B, below.) Somewhat less extreme reduction is seen in the study of functional changes (such as habituation) in very small invertebrate ganglia that consist of only a few identified cells. Toward the other extreme of completeness is the investigation of properties of large brains that have been somewhat reduced by localized impairment of function; this would include studies of the effects of experimental brain lesions in animal subjects and effects of surgical intervention or diseases (e.g., Korsakoff's syndrome) in human beings. At the extreme of complexity is the investigation of intact human subjects; even here a certain degree of simplification is achieved by the design of experimental tasks that limit information, restrict the types of processing to be undertaken, and channel the responses that may be made. In each of these types of subjects or preparations, investigations can be directed toward different levels of analysis and understanding. These may range from attempts at understanding chemical changes taking place in individual neurons to understanding the behavior of ensembles of neurons or the relationships among large neural circuits and structures. Within the intact mammalian brain, investigators may record gross potentials to repeated presentation of a simple stimulus during habituation, record single unit potentials during the same stimulus presentation, make a Fourier analysis of input and output of several single units in a brain structure, or study changed responsiveness of single units during associative conditioning.

Proponents of research with relatively simple systems point out that these may offer opportunity for more searching levels of analysis. It is possible to study such systems rather exhaustively, and one can hope to determine directly all of the important biochemical and electrophysiological processes that take place, whereas in more complex systems basic processes often cannot be analyzed as directly or localized as precisely. It is also held that knowledge gained from the relatively simple systems can easily be applied directly to more complex systems or at least will aid in the formulation of more adequate hypotheses concerning complex systems. To the extent that nature is conservative, basic biological mechanisms may be identical over a wide range of animals. Thus, for development of classical genetics, Drosophila proved to be the subject of choice, and for development of molecular biology, E. coli proved to be excellent. The molecular biologists claim that what is true of E. coli is true of the elephant. Even here, it might be noted that molecular biologists are turning more and more to work with complex cells, including mammalian cells, to study events that do not occur in bacteria. It is with such models in mind that some investigators are exploring relatively simple preparations that they hope will permit a breakthrough in knowledge of the basic neural processes of learning and memory.

Reviewing research on simplified biological systems that might serve as models of neural mechanisms of learning and memory in the vertebrate brain, Thompson, Patterson and Teyler (Annual Review of Psychology, 1972, p. 86) specified three criteria that the simpler system should meet. Let us note these criteria and comment briefly on them: "1. The behavioral properties of plasticity in the model system must correspond to those of intact higher vertebrates." That is, if one is interested in long-term

memory for associative learning, then it will probably not be sufficient to employ a preparation that shows only short-term habituation. "2. Neural mechanisms underlying plasticity in the model system must be amenable to some degree of analysis. Thus, demonstrations of learning in even pieces of insects are of little value if the mechanisms are embedded in unknowable neuropile." That is, there is little point in studying a reduced system unless it offers clear advantages for specific analysis. "3. Mechanisms underlying plasticity in a model system must also be shown to hold for learning in the intact higher organism. This fundamental problem of inference is the greatest weakness of the model systems approach--there is no guarantee that the models will yield anything but interesting games quite irrelevant to an understanding of learning in higher vertebrates." At the very least, research with higher vertebrates is needed in order to test the applicability of formulations reached with simpler systems, and this requires intimate knowledge of the functioning of the higher systems.

2. Formulations in terms of alterations of neural circuits

There is a broad consensus that long-term storage of memory involves changes in neural circuitry, but, as we will see, there is not unanimity even on this general formulation. Among those who subscribe to the hypothesis that memory is stored in terms of changes in neural circuitry, there are differences of emphasis: Some investigators stress biochemical changes at existing synapses, while others stress anatomical changes, including not only modifications in size of junctional regions but also formation of new synapses or resorption of previously existing synapses. Of course the anatomical changes must involve biochemical processes in terms of neural messages, metabolism, and growth, although it is still rare for the same research group to attempt to study both anatomical and biochemical changes in the nervous

system in response to training or differential experience. In part the emphasis on biochemical (and electrophysiological) change versus anatomical change may be related to the type of subject and type of learning being investigated. Thus, research on habituation in identified neurons of invertebrate ganglia has yielded evidence of electrophysiological and presumably also of biochemical changes, but no changes in anatomy at existing junctions have been reported, let alone changes in numbers of synapses. It may be that the anatomy of synapses in small invertebrate ganglia is fixed genetically and is not subject to environmental influence, at least in the postlarval organism. On the other hand, it may be that anatomical changes could be found in invertebrate synapses as a function of experience if investigators attempted to find such effects. After all, it is only in the 1970s that investigators first reported anatomical changes in mammalian synapses caused by differential experience, although such modifications had been hypothesized in the 1890s.

A competing general point of view is that memory is stored in terms of capacity to produce differential patterns of electrical activity, that this capacity is distributed through rather large aggregates of neural tissue, and that the patterns can be "read off" even by cells at a distance from the region of origin of the pattern. Furthermore, it is claimed that the essential phenomena of learning and memory cannot be found or studied in single cells or even in small circuits but require distributed, statistical, global neural function. For a statement of this nonreductionist, nonlocalizationist position and a review of the relevant research, see John and Schwartz (Annual Review of Psychology, 1978, in press). A few of our respondents stated that even according to this view, changed patterns of neural responses must be based upon altered connections among neurons,

so the investigation of biochemical and anatomical changes with learning is not rendered superfluous.

B. Examples of Current Research Approaches

Since research on neural mechanisms of learning and memory is currently being pursued along many different lines, let us examine briefly a few examples. We will first consider study of simpler and more reduced systems and then take up investigation of more complex and complete systems. In each example, we will note the kinds of questions that investigators are attempting to answer with their approach and also the kinds of problems that cannot be solved in this way and that must be referred to those working with other systems. We should emphasize that we are not attempting to be comprehensive.

1. Bases of cell-cell interactions.

It has been suggested by some investigators that basic to an understanding of brain plasticity is knowledge of the molecular bases for cell-cell recognition and interaction. Such investigators typically use systems far simpler than a functioning nervous system. For example, Barondes uses slime molds as a possible model for neuronal cell recognition. In a mixture of slime molds, species specific sorting is observed at one stage of the life cycle. This sorting suggests that a biochemical basis for cell achesion exists. Evidence has been obtained that the protein-carbohydrate binding specificities differ among species of slime molds.

Another example of a model system is the retina of chick embryo, which contains heterogeneous cell groups. Differences in adhesion properties can be shown between the dorsal and ventral cells of the retina. Various biochemical techniques can be used to study the types of molecules which determine the surface properties that cause adhesion.

Immunological approaches coupled with tissue cultures of discrete cell types are also being used to elucidate differences in the surface or membrane properties of developing neural tissue.

Some questions that may be answered by this approach include the following: What are the chemical classes of molecules that are responsible for cell recognition and interaction? Eventually, what are the detailed structures of these molecules? What is the distribution of these molecules on the cell surface? What mechanisms control the production of these coding molecules on the membrane?

Some questions that will be left for other research approaches: How can knowledge of molecular mechanisms of cell-cell recognition and interaction be applied to neural cells? Do these molecular mechanisms underlie formation of synaptic junctions? Can the molecular mechanisms of cell recognition be shown to be sufficiently numerous and precise to account for the highly varied and specific connections of a vertebrate nervous system? In particular, can they account for the connections that are presumed to be formed or altered during learning and memory formation?

2. Study of synapses in a culture of specific cell types.

P. G. Nelson and C. N. Christian of the National Institute of Child Health and Human Development are studying synaptogenesis and synaptic activity in cultures comprised of only two cell types, one presynaptic and one postsynaptic. Populations of cells can be selected according to the degree to which they interact with a second cell type. Formation of synaptic junctions can be studied as a function of induced electrical activity of the neurons and of pharmacological and hormonal environment of the cells. Other investigators are using more complex culture systems with more than

two cell types to obtain information that may be more representative about the specificity of synapse formation.

Some questions to be answered by this approach: Basic processes of synaptogenesis, synaptic connection, and synaptic transmission can be studied with such preparations. Neural cell types can be characterized according to their capacity for interaction with other cell types. Experiments can determine what types and amounts of electrical activity of cells, and what chemical and hormonal conditions, favor formation or maintenance of synaptic connections.

Some questions that will remain for other research approaches: To the extent that different cell types are differentially capable of forming synaptic connections, where are such cells located or grouped in the CNS of higher vertebrates? When chemical and/or hormonal conditions are identified that favor formation or maintenance of synaptic connections, can some of these conditions be found to be produced in the CNS of higher vertebrates? If so, what events give rise to these conditions, and in what locations in the CNS do they occur?

3. Study of simple nervous systems with identifiable neurons

A number of groups of investigators are studying small ganglia or neural networks of invertebrates in which each neuron is identifiable and which display a relatively simple kind of behavioral plasticity--habituation. It may also be possible to study associative learning in some of these systems, which are undoubtedly more complex than had been supposed originally.

Some questions to be answered by this approach: What kinds of synapses--specified in terms of their anatomy, biochemistry, and electrophysiology--show plastic changes (offer possible correlates of learning) and what kinds

do not? At what site(s) in the junctional region do plastic changes occur and what processes are involved (e.g., presynaptic inhibition, changes in availability of synaptic transmitters, etc.)?

Some questions that will remain for other research approaches: How can the cells and processes found to be of interest for learning in simple invertebrate systems be put into correspondence with cells and processes in the central nervous systems of higher vertebrates? Can the mechanisms found to account for a rather simple sort of plasticity (habituation) be used as a basis on which to erect hypotheses about more complex forms of learning in more complex invertebrate or vertebrate nervous systems--hypotheses that can be tested in these higher forms?

4. Fine-grained analysis of changes in synapses and neural circuits caused by training of specific experience.

A few groups of investigators are studying changes in synapses and in neural circuits caused by training or by giving animals differential opportunities to learn in enriched, standard colony, or impoverished environments; this research is being done with rodents. Significant effects have been found at any age at which the differential experience has been given, from preweaning to full adulthood. Several groups are studying changes in synaptic connections and in receptive fields of cells in the visual system caused by restricting visual stimulation (allowing only monocular stimulation) or by giving distorted stimulation (allowing the animal to see only vertical lines or only points of light). Most of the subjects are cats or monkeys. Striking effects have been found, but they can be produced only during a critical period early in the animal's life.

Some questions to be answered by this approach: Do these effects offer a general model for learning and formation of memory traces? Are they closely correlated with learning and memory storage, or can they be attributed to maturation of a sensory system? What is the distribution of effects among specific structures of the mammalian brain? Can similar synaptic effects be produced with other sorts of training that involve different sensory modalities?

Some questions that will remain for other research approaches: How are the synaptic changes produced in terms of biochemical events, involving RNA transcription, protein synthesis, etc.? What kinds of processing of environmental information must occur if memories are to be stored in terms of altered synapses and neural circuits?

5. Study of general chemical and/or electrophysiological processes that occur widely through the central nervous system during information processing, learning, and consolidation of memory.

Widespread chemical changes in the CNS during or after learning are being studied by a number of investigators or groups. The measures include changes in synthesis of messenger RNA and protein synthesis during or after formal trainiing in rodents and in fish and after imprinting in chicks. Widespread changes in evoked potentials have been found in human subjects after training.

Some questions to be answered by these approaches: What sequence of chemical steps is necessary for the formation of long-term memory traces? For example, does encoding of memory always require synthesis of new molecules of mRNA or can existing molecules be used in some cases, for example, when training is strong? How is the consolidation of long-term memory modulated by such factors as the levels of neural activity, attention, motivation, or reinforcement that follow the training? Can information be stored in the form of electrophysiological patterns that are determined statistically and globally without dependence on specific synapses or small circuits?

Some questions that will remain for other types of approaches: To what extent can the observed changes be localized in functional regions of the CNS? What essential roles may be played in learning and memory formation by parts of the vertebrate CNS that do not themselves show chemical or electrophysiological changes during learning and memory formation; may some regions be necessary to facilitate memory storage that occurs in other parts of the brain? How does reinforcement contribute to learning and storage of memory?

6. Detailed behavioral study of information processing, learning and memory in different mammalian species, and in normal, retarded, and brain-injured human beings, using varied techniques, including signal detection and reaction time analyses.

The experimental study of learning and memory started late in the last century with normal and brain-injured human subjects and then expanded to encompass animal subjects by the end of the century. The behavioral study of learning and memory has become a very large field of research, utilizing a wide variety of techniques.

Some questions to be answered by these approaches: Can the facts concerning memory be more adequately conceptualized in terms of distinct stages (e.g., short-term and long-term memories) or in terms of levels and types of processing of information (e.g., maintenance rehearsal and elaborative encoding)? Is all learning basically of one type or are there several distinct phenomena following different laws but lumped together under the general heading of learning? For example, what are relations between classical and instrumental conditioning; does toxicosis conditioning (bait-shyness) follow different laws from other learning? What can the analysis of amnesia in human beings tell us about the structure of normal memory and about the neurophysiology of memory? What tests of learning and memory can best characterize the defects that occur with various kinds of brain damage? What behavioral paradigms may offer the best opportunities for studying neural bases of learning and memory? (These last questions bring us full circle to the preceding approaches.)

III. Problems of Pursuing Research in this Field and Achieving Applications

Although there is considerable optimism among investigators in this field that basic research is showing promise and that there are exciting leads to follow, at the same time there are real problems and obstacles to the pursuit of this research. Some seem to be inherent in the field, while others are imposed from external sources. Beyond the problems of conducting basic research are those of translating some of its advances into application. An understanding of any problem as complex as human learning and memory will require a body of knowledge that in its interweavings and interconnections will probably be only a little less complex than the subject it is attempting to understand. An attempt to indicate this has been made in the previous section when a few examples of studies designed to lead ultimately to an understanding of learning and memory processes have been briefly described. Many readers of this brief survey undoubtedly reacted by saying, "My favorite approach has not been cited." This we will readily acknowledge, but it does serve to illustrate that there are many approaches which must be brought together in order to attain possible solutions.

Processing, storing, and retrieving of information in the nervous system each involves a number of distinct steps. (One respondent suggested that each of these phases probably involves on the order of ten or more distinct steps.) Moreover, the expertise of a number of disciplines is required to study and understand many of these steps--biochemistry, electrophysiology, neuroanatomy, pharmacology, behavioral psychology. Thus the successful investigation of these events demands interdisciplinary collaboration--multidisciplinary, in fact. This is not easy to achieve, since most investigators are still trained in only a single discipline and have little comprehension of what even neighboring disciplines are about--their potentialities, limitations, and preferred habits of work. Presumably the investigators who participated

in the Asilomar Conference were more willing and interested than most to exchange with and learn from members of other disciplines and investigators working at other levels of analysis. Yet in our initial survey we found that most respondents mentioned only one or two research approaches as likely to yield important progress in understanding neural processing and storage of information. Perhaps this exemplifies the saying, "We're down on what we're not up on." Fortunately there are already several multidisciplinary groups working in this field, and a number of younger investigators are being exposed to several of the pertinent disciplines.

Multidisciplinary research is not only difficult to set up but it is necessarily expensive. Here external constraints curtail present research. One of the respondents wrote as follows: "That we are as yet unable to say much about chemical and morphological bases for neural processing and storage of information is because good ideas, proper techniques, and money to support the research are hard to come by. Even with the tools and ideas we have now, we are simply not able to move ahead because funds are tight, especially to support people (pre- and postdoctoral) who want to work in this area."

The lack of funds to support young investigators is especially grave because it may discourage and reduce the numbers of young people coming to this area. Some agencies are cutting down funds of established investigators in order to encourage initial projects of beginning researchers, but this is just robbing older Peter to pay younger Paul. A sustained attack in this important area needs funding for both established investigators and for those entering the field.

Another problem concerning funding is the bandwagon approach of some agencies and foundations which concentrate their support on popular or "safe" areas of research. Some approaches seem to receive more money than is

necessary while others, which also have much to offer, are neglected. Especially when it is realized that neural mechanisms of learning and memory are multiple, involving many stages and levels, it is shortsighted to force-feed some areas and starve others.

Translating research advances into applications involves a further set of problems beyond those discussed above. Applications are usually made by individuals who see a need and who know, or are willing to learn, the research findings that may be drawn upon to solve the need. In the present case, there seem to be few individuals--either investigators or educators--who meet this double criterion. We have found the great majority of investigators in neural mechanisms of learning and memory to have little or no interest in eventual applications of their findings. (We base this statement not only on acquaintance with many investigators but also on attempts to elicit comments on applications during the 1974 Asilomar Conference and in preparation of chapters for publication in Neural Mechanisms of Learning and Memory, 1976.) It is our impression that few potential users of applications--school educators, those in special education of the retarded and handicapped, specialists in rehabilitation--keep up with either behavioral or biological research on learning and memory. This impression is reinforced by a review of Neural Mechanisms of Learning and Memory that appeared in the journal, Educational and Psychological Measurement, 36, 1976. The reviewer noted that "All papers were edited for readers without detailed knowledge of the discipline involved, but educational researchers will still experience difficulties in understanding many of the technical papers." The reviewer cautioned educators "... to stay up-to-date if they wish to consider the matter seriously. Although Thorndike's connectionism and Lashley's mass action and equipotentiality are dated concepts, the reviewer still finds some educationists referring to them as a blueprint for educational policy." In part V below, we will offer a few recommendations to help improve communications between researchers and potential users of applications.

IV. Possible Applications to Come from Research in this Area

Although we realize that prediction is a risky business, nevertheless we are convinced that research in this field is bound to lead to important benefits in preventing or ameliorating the conditions of many who suffer from impaired learning and memory and also in facilitating or improving the learning of normal individuals. Among the kinds of individuals who are likely to be aided relatively soon are children subject to the combination of early malnutrition and social deprivation, some types of retarded children, persons with congenital malformation of the central nervous system, patients suffering from injuries or diseases of the CNS, the aged who suffer from senile decline, and people whose CNS is damaged by drugs (including drugs now being presecribed medically) or by toxic agents in the environment. Applications to improve or facilitate the learning of normal individuals will generally come more slowly because there is less perceived need here, but even at this level we foresee some applications.

We do not venture to offer a timetable of advances or applications, for several reasons. Retrospective studies have shown that applications in science and technology have been founded on earlier basic studies, usually undertaken without any thought for the applications to be made eventually, but the time that has elapsed between a basic discovery and its application has varied greatly from one case to another. Not only is the rate of research progress and application within a field problematic, but also the likelihood of influence of external factors is even more difficult to estimate. Two such external factors are the level of research support, which depends largely on governmental policies, and technical innovations from other fields. The introduction of the computer, for example, has enormously increased the potential of both behavioral and biological research on learning and memory,

but this innovation could not have been predicted from within the field.

We have recently expressed ourselves on this topic in our Introduction to the 1976 publication of the Asilomar Conference (Prospects for application of research on neural mechanisms of learning and memory, pp. xi-xiii). We will attempt here to be more specific in some cases than we were in the Introduction, and we will thereby increase the likelihood of being in error.

A. Applications within the field of research

Research feeds on itself, and especially in the case of a field that is--and must be--studied at many levels and by investigators from many disciplines, it is likely that advances made at one level will, with some delay, lead to improved research at other levels. Thus, behavioral studies may lead to simple but powerful paradigms of training that may be more useful in biological studies than the rather complex instrumental learning that has often been employed for this purpose. Studies of formation of synapses in tissue culture may lead to formulation of new hypotheses of mechanisms of memory storage that can be tested in vertebrate brains. Especially if workers at different levels of analysis and from different disciplines collaborate, or at least are made aware of each others' advances, the first applications will be within the field itself.

Usually, however, we think of applications as being made outside the field of study, and we should turn now to these. Effects of such external applications of research on learning and memory can be divided into two kinds--direct effects upon individual learners, and social effects of improvement in learning. The first of these is the main subject of this sketch, but the second should not be completely ignored here--either for its own importance or because it is likely to have reciprocal influences on application of knowledge in this field to the individual. Only a few specific examples are mentioned; readers will undoubtedly have others to offer.

B. Applications to individuals

1. Combatting effects of malnutrition or specific dietary deficiences on learning and memory.

Perhaps the most tragic of memory deficiencies, because they affect a large part of the world's population, are the interrelated effects due to early malnutrition and the almost invariably associated social deprivation of the millions of the world's poor and hungry. In much of the world, this physical and mental deprivation is due to overpopulation which outstrips available resources. In this country, it is more often due to social factors which probably can be more easily corrected by appropriate behavioral techniques, including both education of parents and appropriate stimulation of the children. It should be noted that malnutrition may also arise, regardless of social factors, in cases of multiple or premature births.

The organic effects of moderate pre- and postnatal malnutrition for the human infant are, fortunately, probably not severe. But frequently this malnutrition goes hand in hand with social or intellectual deprivation, and research is just now beginning the attempt to dissociate the effects. In this area the use of animal models has not brought about as much clarification as in other cases, because malnutrition, in animals as in human beings, causes a combination of motivational and intellectual changes that are hard to disentangle. As Barnes has pointed out, malnutrition leads to apathy which effectively reduces environmental stimulation. Some recent research suggests that behavioral techniques can be as important as dietary supplements in preventing long-term intellectual deficits.

Diet may also be used to prevent occurrence of certain severe defects in learning and memory formation or to treat certain defects. Thus, malnutrition has been implicated in the accelerated decline of neuropsychological

functions in aging. Again, Korsakoff's syndrome has been traced to localized brain lesions caused by lack of B vitamins in alcoholism. As the neurochemistry of learning and memory becomes better known, along with the specific nutritional requirements of specific brain regions, it may well become possible to prevent or to counteract other kinds of impairment of learning and memory.

2. Alleviating and preventing mental retardation

Some kinds of mental retardation are known to be caused by disease, malformation of the brain, or birth trauma, but in many cases the neurological cause of the deficient behavior is not yet known. In some cases of apparent retardation, the basic problem is emotional or motivational, rather than intellectual. Further study of learning problems in children should yield tests that can distinguish between these sources of difficulty in learning. Where the cause has been established, programs of alleviation or prevention can be devised. Thus, many states now require routine screening of all newborn infants for phenylketonuria, and in cases where PKU is detected, a special diet in the early years can prevent appearance of the abnormality. If specific proteins are found to be necessary for memory formation, as some investigators now suppose, then it may be discovered that the lack of these proteins is responsible for some types of mental retardation. In that case, administration of these proteins might provide a specific therapy, as insulin does for diabetes. When the genetic basis of the cerebral defect has been established, occurrence of the condition can be prevented through genetic counseling, as in the case of Tay-Sachs disease. Eventually it should become possible to correct such genetic defects by means of "genetic engineering."

In cases where the organic basis of retardation is not yet known, it is difficult to design effective means of therapy or prevention. In the absence of known causes, various therapies are promoted which are claimed to be based on neurological knowledge or principles but which in fact are purely hypothetical. Some current research is being done to attempt to classify learning potentialities of children in terms of EEG activity (resting responses or evoked potentials), and they may aid in choosing appropriate educational strategies for the individual learner. As we gain further knowledge of the neural bases of learning and memory, investigators will have better ideas of types of anatomical and biochemical abnormalities of brain that could cause impaired learning and memory. Thus there have been a few recent reports that some retardates may be characterized by abnormal development or disappearance of dendritic spines or by decreased concentrations of synaptic vesicles. If particular neural abnormalities can be demonstrated to cause various kinds of retardation, this will be a major step toward devising appropriate therapies and toward determining the genetic basis of the condition.

3. Promoting recovery of function after damage to the nervous system

Increased knowledge of the processes underlying synapse formation in learning and memory and of neural sprouting could be important aids in promoting recovery of function and rehabilitation after brain damage. At present there is both a great deal of discouraging information that injury to the brain leads to persisting behavioral defects in learning and memory and in information processing, but at the same time the literature contains many cases of striking recovery after serious damage to the brain. In a number of cases, the striking examples of recovery have been attributed to energetic programs of retraining. Recovery from a variety of motor disorders

of neurological origin has been aided by providing adequate sensory feedback. While the status of biofeedback suffers somewhat from premature and exaggerated claims, these techniques are likely to develop into powerful therapeutic tools (see Miller, Annual Review of Psychology, 1978). A promising possibility may be the use of spinal conditioning to promote bladder control in paraplegic patients.

Further research on methods of training, coupled with knowledge about conditions that facilitate growth of neural connections, could lead to important gains in this area. Some respondents cited research on recovery of function as an extremely promising area that should receive enhanced support and attention.

4. Preventing or retarding senile decline.

Almost as certain as "death and taxes" is aging, and senior citizens represent an increasing proportion of the population. Although there is great variability among individuals, almost inevitably aging is accompanied at some point by a decline in mental abilities, even in the absence of major brain damage due to cerebrovascular accidents, malignancies, etc. Little is understood concerning the causes of mental deterioration with age, and even less concerning methods of alleviating the effects. More adequate studies of brain and behavior during aging could lead to better diagnostic assessments on which to base programs of prevention and rehabilitation.

To what extent is the apparent decline due more to social and psychological factors--such as a lack of mental challenge--and to what extent is it organic? An understanding of the causes might enable us to design social programs of moderate cost which would save billions of dollars in institutional care as well as untold suffering. Perhaps a more basic understanding would stimulate the design of psychosocial or nutritional progrmas or drugs that would alleviate, at least in part, this common and widespread problem.

5. Using drugs and/or hormones to improve learning and memory; avoiding drugs that impair learning and memory.

Pharmacological agents offer both promise and dangers. Use of stimulant drugs following training to enhance the formation of long-term memory has proved effective in animal studies, so prudent application of these methods is to be expected in some cases of slow learners or brain-damaged individuals. Hormones are also being found to facilitate learning and memory storage, and some cases of deficient learning and memory may be traced to homornal imbalances. The possibility of development of dependency on drugs indicates that great caution must be used in pursuing such therapeutic attempts. Whithin certain limits, the use of hormones is less likely to produce undesirable side effects than is the use of nonphysiological synthetic compounds. The establishment of biochemical bases of learning and memory formation could lead to a more rational selection of therapeutic agents than is now the case.

Several types of long-term damage to the nervous system may be caused by drugs. In some cases, the damage occurs prenatally through placental transfer as a result of the mother's use of the drug. Only recently is there an appreciation of the potential effects of drugs (and even food additives) which may lead to nervous system damage and consequent impairment in learning ability. It is now recognized that the infant is particularly vulnerable to food additives, and as a result certain additives have been removed from infant foods (e.g., monosodium glutamate). To what extent these, and other compounds, may affect the more mature nervous system is less well understood.

At a later time in life, individuals, either voluntarily or frequently on the advice of physicians, take a variety of drugs that act on the nervous system. Many of these drugs have powerful effects on the nervous system;

some are damaging, some are addicting, but the mechanisms of action of many, if not most, are only partially understood. More widespread concern for possible effects of drugs on learning and memory will undoubtedly lead to findings that can be applied. For example, it has recently been shown that marijuana does not seem to affect retrieval of previously learned material but that it does appear to impair storage of new information.

Many drugs are introduced into commerce without an adequate assessment of possible neurological effects, especially effects that appear only after long-term use, although the drugs may have been tested extensively to determine their potentials for carcinogenicity or teratogenicity. Drugs that are designed to inhibit key steps in nucleic acid and/or protein synthesis are frequently used in cancer chemotherapy. Since inhibitors of protein synthesis and certain other drugs have been shown to impair formation of long-term memory storage in animal experiments, physicians who use such drugs clinically should be alerted to watch for such possible effects in their patients. Beyond this, a research program with such patients could have both applied and theoretical value.

6. Detecting toxic agents in the environment

Improved clinical tests of learning and memory might aid in the detection of toxic agents in the environment. With the increasing concern for possible effects of toxic agents in industry and elsewhere in the environment, tests of learning and memory could be added to screening devices. Among substances already know to affect mental functioning are lead, mercury, arsenic, and insecticides. Better knowledge of the regions of the brain important for learning and memory, coupled with animal experiments that tested effects of suspected toxic agents on these regions of the brain, could help to prevent such damage.

7. Applications to school education of normal children

The applications described thus far have all been for the alleviation or prevention of various kinds of impairment. Applications of neuro-behavioral research to learning and memory of normal individuals will probably be less frequent or at least will tend to occur further in the future. One obvious reason is that it will be more difficult to secure funds to improve the education of normal individuals, where little need is generally seen, than for improvement of learning of retarded or handicapped individuals. Even for the normal, however, we can see some applications of research in processes of learning and memory.

Findings of experimental psychology are now being translated into the classroom. For example, recent research has shown that even normal college students can benefit in learning foreign language vocabulary by being presented with "keywords" that link the sound of the foreign word to a visual image. Further research is now being done to apply this derivation from experimental psychology to a variety of practical learning situations. Many other findings from the experimental psychology of learning can probably be applied in the classroom. Some examples are (a) the fact that students who organize material learn more rapidly than those who do not, (b) the value of "chunking" familiar material to store it as a unit in memory, (c) the use of distributed rather than massed practice in learning of complex material. Training in the use of mnemonic systems has been shown to be of benefit not only to students but even to some patients with diseases of the central nervous system, and more general use could be made of such systems. Thus, many applications can now be made from already established behavioral findings about learning and memory, and such application should be encouraged so that current students can benefit from successful research of the past.

Beyond this, we can picture in a science-fiction manner applications of recent research on periodicity of neural processes and of behavior. The 24-hour (circadian) rhythm has been related to many aspects of neural activity, physiological processes, and behavior. For example, it has been shown in rodents that susceptibility to many pharmacological agents varies markedly during the 24-hour cycle, and ability to learn and consolidate memory also shows strong cyclical changes. During the day there is also an ultradian cycle whose period is about 90 minutes long in adult human beings. This ultradian cycle was first detected during sleep as the periodicity of dreaming, Rapid Eye Movement sleep, and its correlates in the electroencephalogram (EEG). Then the ultradian cycle was also observed during wakefulness, in terms of periodic changes in attention, tendency to daydream, and oral behavior. The ultradian cycles are shorter in children than in adults and mature gradually. In the typical elementary school classroom, there are children with cycles of different lengths, and at any given moment different children are in different phases of their cycles. One can picture the possibility that in the future children in large schools will be grouped into classes partly in terms of the maturity of their ultradian cycles; perhaps the lengths of class periods will also be related to the ultradian cycles of the students. Gazing further into the future, one can even imagine that suitable exercises may be devised that will help to synchronize the rhythms of classmates, so that the whole class would be ready to direct full attention to new material at one phase and to be ready to take a break at another part of the cycle. If synchronizing rhythms for the whole class proves difficult to achieve (and there may be survival value to the persistance of individual differences in rhythms), then splitting the class into work groups according to individual rhythms may be a feasible and useful alternative. EEG recordings might be used at first to determine ultradian rhythms of

individuals to form classes or work groups, but simple behavioral tests will probably be devised eventually to assess the rhythms accurately and to make such assignment economical and practical. If the future educational emphasis is on individual instruction rather than class groups, it will still be useful to schedule individual sessions in relation to peaks of altertness.

IV.

C. Social effects of applications of research on learning and memory

Some social consequences of research in this field will probably be purely beneficial, but other effects may cause secondary difficulties or complications about which advance consideration may be worthwhile.

1. Beneficial effects

Among the purely positive results of such research are several that we have just described in Section IV B: reducation in the number of mental retardates, fewer children handicapped by the combination of early malnutrition and social deprivation, reduction in the incidence and rate of senile decline, fewer cases of impairment of the central nervous system by drugs and toxic agents, and improvement in the rapidity and final level of recovery after brain injuries.

Another benefit, not described earlier, is an ecological application which shows that studies of learning and memory may have important "spin-offs" in areas that are apparently far-removed from the initial focus of the research. This example comes from studies of food-aversion (bait shyness) in which an animal quickly learns to associate noxious physiological consequences with a particular food. The application is use of these findings for control of predator (e.g., coyote) attack on livestock (e.g., sheep). Although the

sheep kill of properly managed flocks is probably small, nonselective distribution of poison bait is frequently used to kill off the coyotes. This has the liability of putting poison into the whole food chain. To the extent that coyotes are killed, it also upsets a natural balance in which coyotes control the numbers of squirrels, rabbits, grasshoppers, etc. which, if unchecked, can harm the range. An alternative may be selective control of coyote attack by use of aversive conditioning. Young lamb carcasses can be baited with chemicals such as lithium chloride which will make the potential predator sick and result in its subsequent avoidance of lambs. It appears that female coyotes will teach this avoidance to their young. Thereby, a selective control of predation may be achieved without the ecological hazards associated with the indiscriminate and widespread use of poisons.

2. Mixed consequences of improvements in education

If knowledge of neural mechanisms of learning and memory leads to introduction of techniques that can substantially improve the learning and memory of normal, healthy individuals, this could lead to mixed social consequences. Some indication of the effects can be gained from considering the consequences during the last sixty years of making public education widely available and prolonging it into college and of the increasing scope and expertise of the mass media. By the time of the Second World War, it was found that the Army intelligence tests prepared during the First World War were so simple as to be no longer appropriate; that is, the effective intelligence of the American population had been raised significantly in a generation. This increase in knowledge and skill was undoubtedly a large factor in the surge in both production and consumption in the United States. Similar changes occurred in the other advanced nations but not to the same extent in the developing or underdeveloped nations, so

an important consequence of improved educational techniques was to widen further the gap among nations. In several countries of Western Europe, a source of personal unhappiness and of social and political instability during the present decade has been the large and increasing number of university graduates who have not been able to find employment related to their field of advanced studies. Similar personal--but not yet political--effects have begun to appear in the United States.

We mention a few such problems not to suggest that researchers refrain from studying neural mechanisms or that educators and others refrain from applying the findings, and not to suggest that the problems are insuperable, but rather because we believe that the problems that will be entailed deserve attention and forethought.

V. Suggestions to foster development of research on neural mechanisms of learning and memory and applications thereof.*

From the material in Sections II-IV, as well as from specific comments of respondents to our surveys, we draw the following suggestions.

A. Support Research along a Number of Directions, at Several Levels of Analysis, and with Several Types of Systems

There is now an active community of researchers in this field, and there is a general feeling of optimism that current research approaches and facilities should permit sustained progress in unraveling the mysteries of the mechanisms of learning and memory. But some respondents stated that the decreasing level of financial support is a serious obstacle to continued research in this direction. Many of the workers feel that understanding of learning and memory are so important to understanding human and animal behavior, and that such important applications are likely to come from this research, that this should be a priority area.

It does not seem to be desirable to concentrate support on one or a very few research approaches, in the hopes that a breakthrough is likely to occur there. Only one of our respondents mentioned the possibility of a breakthrough, and the direction that he singled out was challenged, in a simultaneous letter from another expert, as having drawbacks for research. Although a breakthrough may be made, it seems impossible to predict which of several promising approaches may yield this result. It would seem best, therefore, for governmental agencies and private foundations to provide adequate support for a number of levels and directions of research, putting main reliance on the excellence of the investigators and on the thoughtfulness and originality of their proposals. One respondent put it in these

* Important related material on social problems that may be aided by research on neural plasticity, current funding and suggestions concerning funding will be found in the June 1977 Neuroscience Newsletter which reached us after the completion of this report.

terms:

> "In my opinion...we presently need a multidisciplinary, many-preparation attack on the subject of learning in order to uncover the underlying biological principles regardless of...whether these principles are going to be the same in the various animal groups. Most importantly, we need new, experimentally useful ideas to guide research, even if in the long run our efforts serve only to shoot them down."

There is a specific need to support research that attempts to span levels and disciplines and that seeks to bridge between specialized approaches.

1. Possible priorities for support of basic research by NIE

A few respondents commented that our draft of May, 1977, was too broad in suggesting a scope and in implying an amount of support that are appropriate to the whole U.S. effort in this direction. They urged us to make recommendations appropriate to the National Institute of Education. Accordingly, we are making here some suggestions in this regard; it should be noted that these recommendations are those of the two authors of this report and have not benefitted from review by our colleagues.

We realize that most of the research support granted by NIE will continue to be for applied and educational activities. It would seem natural for NIE also to support basic research in areas that are likely to yield applications relatively soon. We believe that this is true of two kinds of research: (a) experimental psychology of learning and memory, which is already yielding applications as noted in Section IV B above; (b) research in neural mechanisms of learning and memory conducted with mammalian subjects, such as those described in Sections II B, 4-6; this would include studies such as those of learning and memory in brain-injured human beings, research on biochemistry of learning in intact mammals, and studies of changes induced in the brains of mammals by training. Support in these areas would not only

foster progress of research that is likely to provide applications, but it would also help to sensitize members of NIE and educators to the advances being made along these lines of research, and this in itself could hasten applications.

B. Improve feedback between granting agencies or foundations and those who apply for grants

Sluggish and inadequate feedback impairs the present system of communication between applicants for research support and agencies or foundations that offer support. Although government agencies now provide information about comments and judgments of study committees and external referees, this may be months in coming, and some private foundations refuse to provide such information. It seems evident that the system would operate better if the grounds for decisions were made available to applicants fully and rapidly. In a recent and thoughtful study of peer review by NIH, 1976, the greatest cause of dissatisfaction by far was the long period between submission of a grant application and the decision on funding.

Beyond this, we would urge that a channel be set up to allow communication <u>during</u> the decision process. Often the rating of a project is influenced by questions about one or two specific points or by doubt about interpretation of a paragraph in an application. It should be possible to inform the investigator that his or her application will be coming up for committee discussion on one of two dates and that the investigator should be available during those days to respond to a telephone inquiry. In that way, questions could be cleared up readily, and there would be much less risk of ratings being based on misunderstandings that, under the current system, may be resolved only months later, if at all.

Some aspects of the NIH Committee recommendations may still not meet all

of the problems or dissatisfactions of applications. For example, retaining a normal 4-year term of membership on initial review boards may make their composition too rigid and lock out certain applications for many years. But perhaps the greatest problem is that the low level of current funding is simply inadequate for the community of investigators studying neural processes of learning and memory. Faced with this constraint, committees may resort to nit-picking in order to select 10% among many grant applications when perhaps 50% are fully worthy of support on their scientific merit.

C. Support Advanced Training of Investigators, Especially Interdisciplinary Training.

To foster future advances in research, it will be important to prepare young researchers, not only within the disciplines that now contribute to this field, but also by providing opportunities for interdisciplinary training. Researchers with an advanced degree in one pertinent discipline should be encouraged and aided financially to gain postdoctoral experience in another contributing discipline.

D. Provide for Positions for Young Researchers

The present dearth of career openings for young scholars and researchers is a threat to the future of research on neural mechanisms of learning and memory, just as it is in many other fields at present in the United States, Canada, and Europe. Action must be taken to provide suitable positions lest a generation be lost to research. Some of these investigators might be encouraged to consider positions in applied research or as consultants to those applying research in this field, and this could help to improve the quality and value of applications. Fluctuations in both supply and demand should be moderated. We know that the problem of positions is being considered

in many quarters and that solutions are being suggested, so we will not go into it further here.

E. Encourage Exchanges between Researchers of Different Disciplines and Working at Different Levels.

Since related problems are being studied by members of several different disciplines and at a number of levels of analysis, it is important to foster exchanges. Techniques developed for one purpose may also be useful at other levels. It is uneconomical, to say the least, if behavioral techniques that have been worked out by psychologists have to be rediscovered through trial and error by physiologists or biochemists. Also, discoveries made at one level of analysis or with one type of preparation may be applicable or may stimulate formulation of valuable hypotheses at another level, once they are known.

One mechanism to encourage interdisciplinary exchanges is to hold working conferences that bring investigators together for a week or more. This fosters a depth of comprehension and also personal understanding. Visiting fellowships to other laboratories provide opportunities for more thorough exchange. Interdisciplinary courses or seminars can bring together not only investigators but also their students.

F. Encourage Potential Users of Applications to Become Better Acquainted with Recent and Ongoing Research.

We saw evidence in Part III that researchers and potential users of applications have little contact and little understanding of the state of each other's fields. How to bridge this gap and improve communications is a difficult problem and one for which we cannot pretend to offer expertise A few rather obvious suggestions would be the following:

Publications reporting on the state of the art, such as Neural Mechanisms

of Learning and Memory, may be of help, and more simplified or popular accounts may also be useful. Educators with background in the relevant sciences might be in the best position to prepare reports that would be useful for other educators. Conferences bringing together both researchers and prospective users of research might be helpful, but participants should undertake advance preparations in order to be ready to understand each other's points of view. Such conferences could also be useful to agencies like NIE in defining areas of research to support and priorities.

It could be helpful if prospective users of applications defined their needs and made explicit what kinds of aid would be most beneficial in their fields; this might be done in conferences, in published discussions, or in symposia or workshops at national meetings such as the annual meeting of the Society for Neuroscience or AAAS. Such statements of needs might guide people in applied areas as they peruse the research literature. Also, statements of needs could be published from time to time in journals such as Science, Nature, and Scientific American where they might be read by investigators of neural mechanisms; investigators might occasionally spot possibilities for application of research in their field.

Providing some basic researchers with knowledge about practical or clinical problems may encourage them to spend part of their time on such applied problems and on bridging gaps. Similarly, providing opportunities for some educators to get first-hand acquaintance with ongoing research could help them to envisage possible sources of applications. Funds for applied research and for applications might help to support laboratories that do both basic and applied research. Finally, popular accounts of applications of research are important to give the public an understanding of how basic research leads to pay-offs, and this is helpful in assuring continued long-term financial support.

G. Support Tests of Proposed Applications of Research on Neural Mechanisms of Learning and Memory

To facilitate the flow from basic research to application, financial support should be made available to test proposed applications. At the same time, support of basic research must continue, in order to provide the foundations for further and more advanced applications.